A cladistic analysis of *Lithasia* (Gastropoda: Pleuroceridae) using morphological characters

Russell L. Minton[1]
Department of Biological Sciences
University of Alabama
Tuscaloosa, AL 35487 USA

ABSTRACT

The classification of pleurocerid snails and other freshwater mollusks has historically been based on morphological characters. Despite years of taxonomic work on pleurocerids, no single work includes all recognized taxa from a given group and only a few systematic treatments of the family or individual genera exist. Modern methods of phylogenetic systematics have shown that some morphological traits do not support historically accepted mollusk classifications. If analyses of morphological characters do support current taxonomic hypotheses, then the classification of these groups can be considered as stable. If not, our approach regarding diagnostic characters for these groups must change. This paper uses 25 shell and radular characters in a cladistic analysis of the pleurocerid genus *Lithasia*, and compares the findings to previously suggested classifications of the group. Cladistic analyses do not support any current or historical classification of *Lithasia*. However, these morphological characters are found to roughly delineate *Lithasia* and other extant pleurocerid genera, challenging previous works that suggest such characters have limited utility.

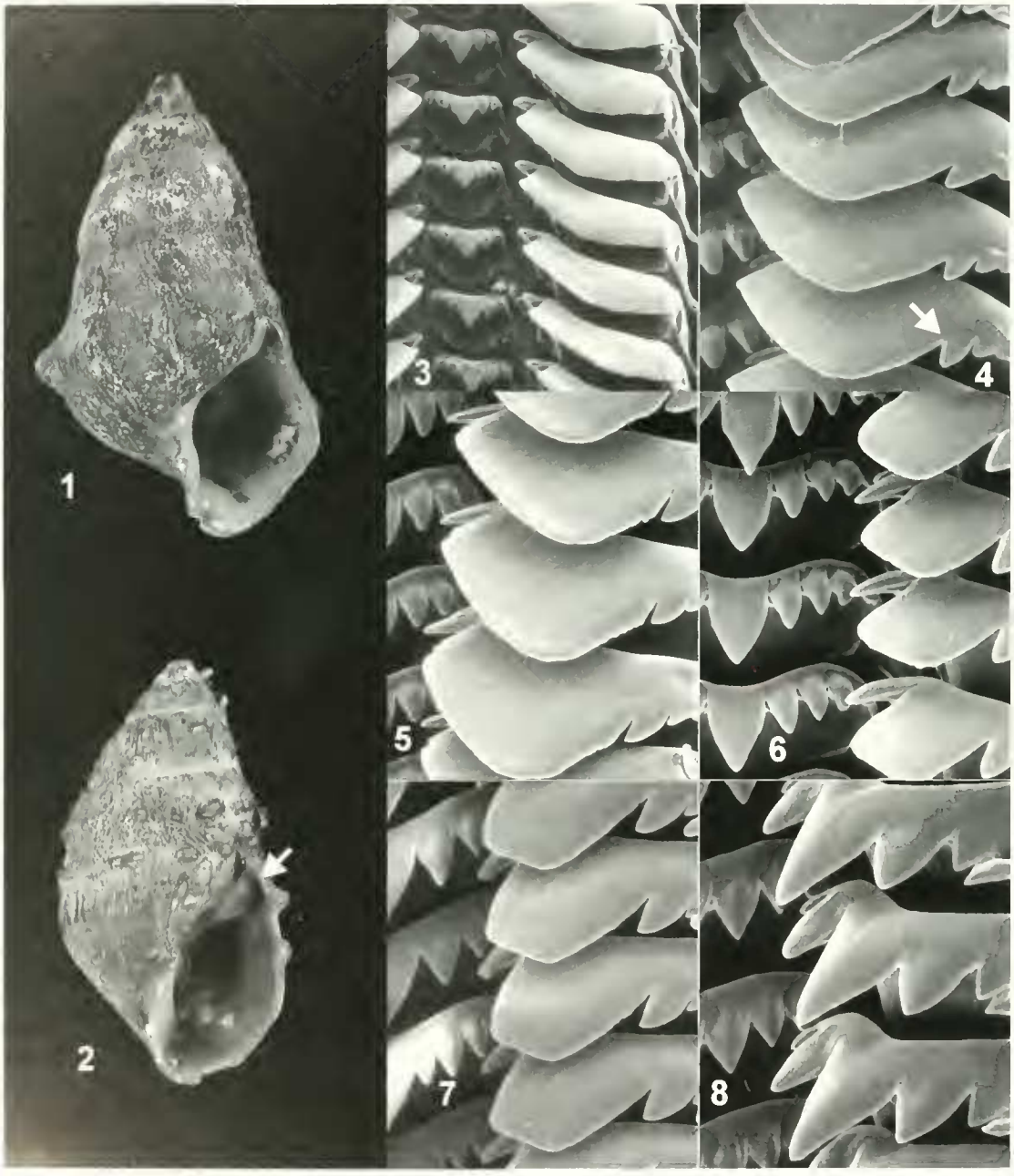
INTRODUCTION

Historically, the classification of freshwater mollusks has relied heavily on morphological features such as shell, soft anatomy, and reproductive structures (e.g., Tryon, 1873; Heard and Guckert, 1970; Davis and Fuller, 1981; Burch and Tottenham, 1980). This is particularly evident for pleurocerid snails, where shell features account for the majority of diagnostic characters used in the taxonomy and classification of the group. One group of pleurocerids that has been classified on the basis of shell characters is *Lithasia* Haldeman, 1840, a genus of large river snails found throughout the Cumberland, Ohio, Mississippi, and Tennessee River drainages.

Species of *Lithasia* possess conic to ovate-conic shells with fusiform apertures, a posterior callus on the parietal wall, and frequently some degree of sculpture on the body whorl (Burch, 1982). Most species were described initially as *Melania*, and classified according to shell characteristics such as shape and sculpture. Haldeman (1840) erected *Lithasia* and designated *L. geniculata* Haldeman, 1840, as the type for the genus and later erected *Angitrema* (1841). Presence of posterior and anterior calluses united *Angitrema* and *Lithasia*. The primary characters separating the genera were that *Angitrema* shells were spinous and had apertures with an anterior sinus, while *Lithasia* shells lacked sculpture and the aperture was not as distinctly channeled in front as the typical *Angitremae* (Tryon, 1873). Goodrich (1921) supported Pilsbry and Rhoad's (1896) reduction of *Angitrema* under *Lithasia*, and *Lithasia* subsequently has stood as a single genus. Goodrich (1940) recognized four separate groups within *Lithasia*, based primarily on peculiarities of shell sculpture. In the 1970s, authors suggested taxonomic revisions of the genus, placing all members in *Io* (Davis, 1974) or *Pleurocera* (Stansbery, 1971; Stein, 1978). Burch and Tottenham (1980) recognized *Lithasia sensu stricto* and *Angitrema* as subgenera of *Lithasia* based on position of sculpture on the body whorl (Burch, 1982), and not according to the original diagnosis, while Turgeon et al. (1998) followed Burch in recognizing *Lithasia* as one genus.

Authors have historically assembled pleurocerid genera based on grouping taxa with shared shell characters. Such is the prevalent approach found in the literature published over a period of 150 years, and no analyses of these characters exists for *Lithasia* or any other pleurocerid genus. This may be a result of the lack of uniform information found in the literature. Different authors rarely provided comparable levels of qualitative or quantitative data in their original descriptions, and seldom used terms and expressions that may or may not have the same descriptive connotations (e.g., tapering versus broadly conic shells), making it difficult for readers to draw comparisons between works. Many descriptions were based on one or a few shells, juveniles, or partial shells given to the author, and radulae were not included in these descriptions. Finally, descriptions were subjective based on the experience of the author, the amount of variation they accepted, and their understanding of the other taxa in the literature. Given the current state of freshwater mollusk taxonomy in general and pleurocerids specifically, and the fact that morphological characters are still used to confirm taxon identity, anal-

[1] Current address: Department of Zoology, Invertebrate Division, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605 USA, rminton@fieldmuseum.org.



Figures 1–8. Illustrations of selected characters and character states used in the cladistic analysis of *Lithasia*. **1.** *Lithasia armigera* showing elongate aperture (2:2) and presence of anterior (7:1) and posterior (6:1) calluses on the columella. **2.** *Lithasia verrucosa* showing umbilicus, body whorl (5:1) and posterior lengthening of aperture (arrow; 10:1). **3.** Absence of cusp next to lateral tooth (19:0). **4.** [illegible] cusp next to lateral tooth (arrow; 13:1). **5.** Lunellar main lateral cusp (19:0). **6.** Rectangular main lateral cusp (19:1). **7.** Trapezoidal main lateral cusp (19:2). **8.** Triangular main lateral cusp (19:3).

yses of these [illegible] employing modern techniques is prudent. M[illegible]s of phylogenetic systematics have shown that [illegible]phological traits do not support historically [illegible] gollusk classifications (Graf, 2000; Lydeard et al., 2000). If analyses of morphological characters do support current taxonomic hypotheses, then the classification of these groups can be stabilized. If not, our approach to [illegible] diagnostic characters for these groups must change. Phylogenetic taxonomies of this kind have been advocated in several studies (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; Bryant, 1996; Sereno, 1999; Lydeard et al., 2000).

Further complicating this problem is that pleurocerids, in a similar fashion to what happens to many other freshwater invertebrate groups, are experiencing declines in their number of species and individuals caused by river impoundment, habitat degradation, and poor land-use practices (Stein, 1976; Bogan et al., 1995; Lydeard et al.,

1997). For example, in the Mobile Basin, one genus (*Gyrotoma*) and approximately 31 other species are presumed extinct (Stein, 1976; Bogan et al., 1995; Lydeard and Mayden, 1995; Lydeard et al., 1997). Even with the loss of diversity in the family, only five of 156 recognized pleurocerid species (Turgeon et al., 1998) are listed as either endangered or threatened as of May, 2001 (U.S. Fish and Wildlife Service). If morphology alone is to be used in identification of these imperiled taxa, then analyses of these characters gain even more importance. A lack of such analyses can hinder efforts to recognize, manage, and conserve distinct taxa (Waples, 1991; Mayden and Wood, 1995) within these affected groups.

The goal of this study is to compile shell and radula characters from *Lithasia*, analyze them using cladistic techniques in order to test historical and modern classifications of the genus and its species composition, and to determine possible relationships of the genus and its taxa to other pleurocerids based on those analyses. Potential changes to the taxonomy of *Lithasia* based on these analyses and the utility of using these characters in pleurocerid classification are discussed.

MATERIALS AND METHODS

Specimens for the study were either collected live or borrowed from museum collections (Appendix 1). Shell characters were taken directly from specimens. Radulae were extracted, cleaned, and prepared according to the method described by Holznagel (1998), viewed using a Hitachi S-2500 scanning electron microscope, photographed, and analyzed. For *Lithasia*, at least one representative from each recognized species and subspecies (Burch and Tottenham, 1980) was included. Specimens of selected taxa representing five other extant pleurocerid genera (*Elimia*, *Io*, *Juga*, *Leptoxis*, *Pleurocera*) were also included (Appendix 1). Data consisted of a matrix of 25 characters (Appendix 2, Figures 1–8) coded as either binary or multi-state (Appendix 3), and analyzed phylogenetically under maximum parsimony with NONA 2.0 (Goloboff, 1998) using the following settings: unordered data, 100 replicates, with *Juga silicula* and *Melanoides tuberculata* Müller, 1774, as outgroups. *Juga* is basal to the rest of the North American Pleuroceridae (Holznagel and Lydeard, 2000) and *M. tuberculata* was chosen as a more distant outgroup. Jackknife analysis (37% deletion, 1000 iterations of 10 replicates each) was performed in NAC (Farris, unpublished; Farris et al., 1996) to test the stability of the data. A strict consensus tree mapped with characters was produced with WinClada 0.9.99m24 (Nixon, 1999). The analysis was run twice, once using shell characters alone and once with all characters combined. Because most previous classifications (e.g., Tryon, 1873; Goodrich, 1940) were based on shell characters only, they were analyzed separately and combined with radula data.

Once the classification hypothesis was established, it was compared to five different classification schemes proposed by previous authors (Appendix 4):

A. Lithasia represents a single genus. This assumption follows the current (Turgeon et al., 1998) view of the genus.
B. Lithasia represents a single genus comprised of two subgenera, *Lithasia sensu stricto* and *Angitrema*, *sensu* Burch and Tottenham (1980). This classification is commonly used as a starting point in pleurocerid studies (e.g., Lydeard et al., 1997; Holznagel and Lydeard, 2000). Burch and Tottenham's (1980) genera and subgenera differ in species composition from those of Tryon (1873).
C. Lithasia represents a single genus comprised of four species groups based on peculiarities of the nodulous sculpture (Goodrich, 1940). *Lithasia hubrichti* Clench, 1965, had yet to be described and is included in Group 3 based on Clench (1965) allying it to *Lithasia verrucosa* (Rafinesque, 1820).
D. Taxa presently included in *Lithasia* belong to one of three genera: *Lithasia*, *Angitrema*, or *Anculosa*, *sensu* Tryon (1873). In this case, the original descriptions of *Lithasia* and *Angitrema* are used to group taxa based on shell characters. Tryon failed to include *Lithasia curta* (Lea, 1868), and *Lithasia hubrichti* had yet to be described. Both species are included in Tryon's *Angitrema* based on their nodulous shell sculpture. *Lithasia geniculata pinguis* (Lea, 1852) = *Anculosa pinguis*.
E. Taxa presently included in *Lithasia* should be considered species of *Io* based on developmental characters, *sensu* Davis (1974). *Io* Lea, 1831, has precedence over *Lithasia* Haldeman, 1840, and *Angitrema* Haldeman, 1841.

A sixth scheme, Stein's (1978b) recommendation that all *Lithasia* be considered *Pleurocera*, is not treated here as it is nomenclatural, not taxonomic, and has since been resolved by the International Commission on Zoological Nomenclature's decision to make *Pleurocera acutus* the type species of the genus (Melville, 1981; see discussion in Bogan and Parmalee, 1983). Characters supporting relationships in the parsimony analysis were compared to characters that grouped species in the other classifications.

RESULTS

Maximum parsimony analysis of shell characters alone yielded 372 trees of 27 steps (Figure 9). *Lithasia* was rendered non-monophyletic by the placement of *Lithasia geniculata pinguis* in the clade of *Leptoxis* species and the placement of *Lithasia obovata* (Say, 1829) in a polytomy of (*Io* + some *Elimia* + (*pinguis* + *Leptoxis*) + remaining *Lithasia*). Analysis of all characters yielded 20 trees of 107 steps that rendered *Lithasia* non-monophyletic (Figure 10). *Lithasia geniculata pinguis* specimens were basal to a clade of *Leptoxis* species supported by a teardrop-shaped aperture, and *Lithasia obovata* was nested between clades of *Pleurocera* and *Elimia* species near the base of the tree. The remaining *Lithasia* taxa formed a clade with *Io* supported by three characters:

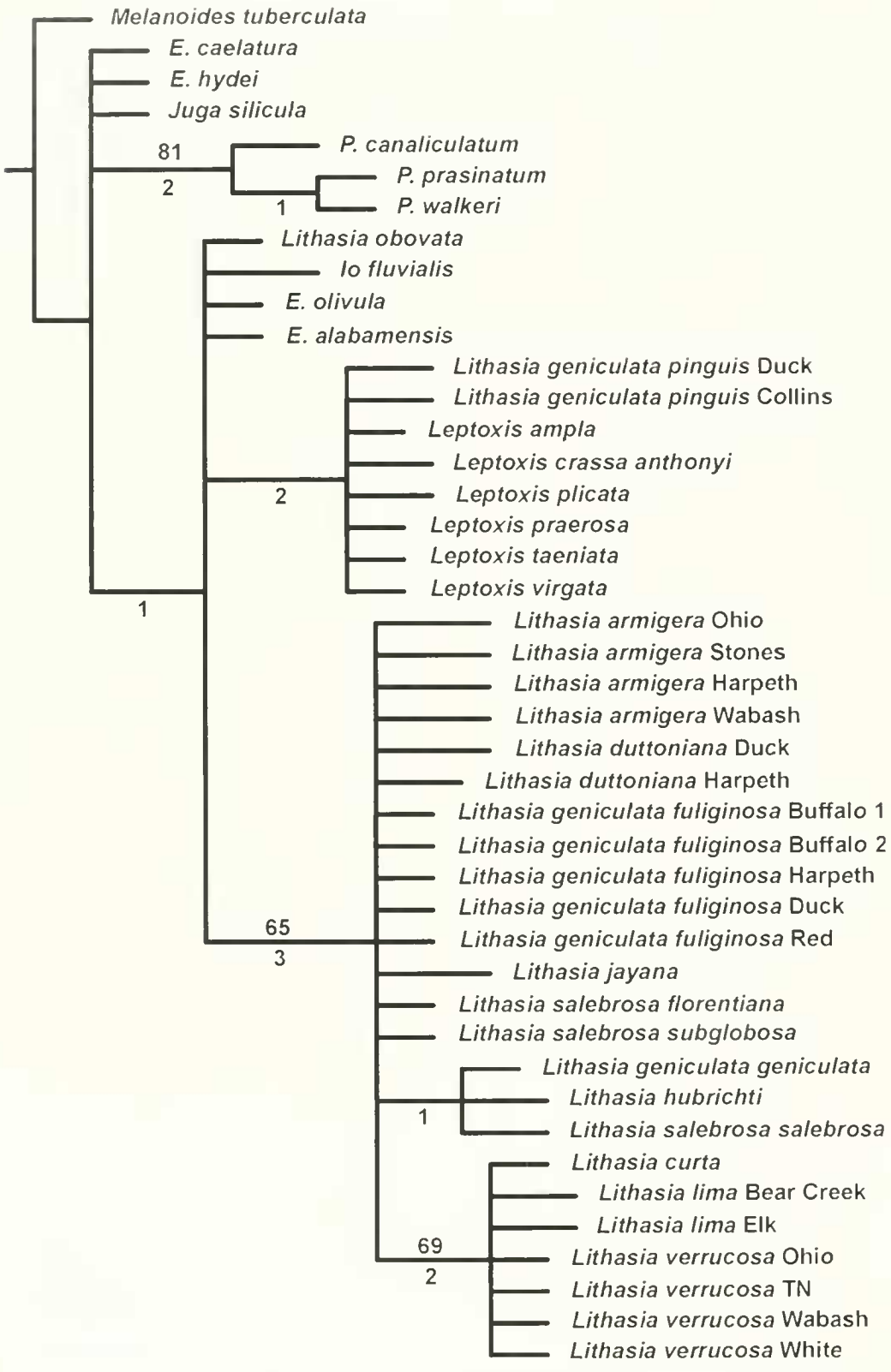


Figure 9. [illegible] Strict consensus of the 372 most parsimonious trees (27 steps, CI = 0.74, generated using shell [illegible] indices > 63% above nodes, number of unambiguous synapomorphies below nodes.

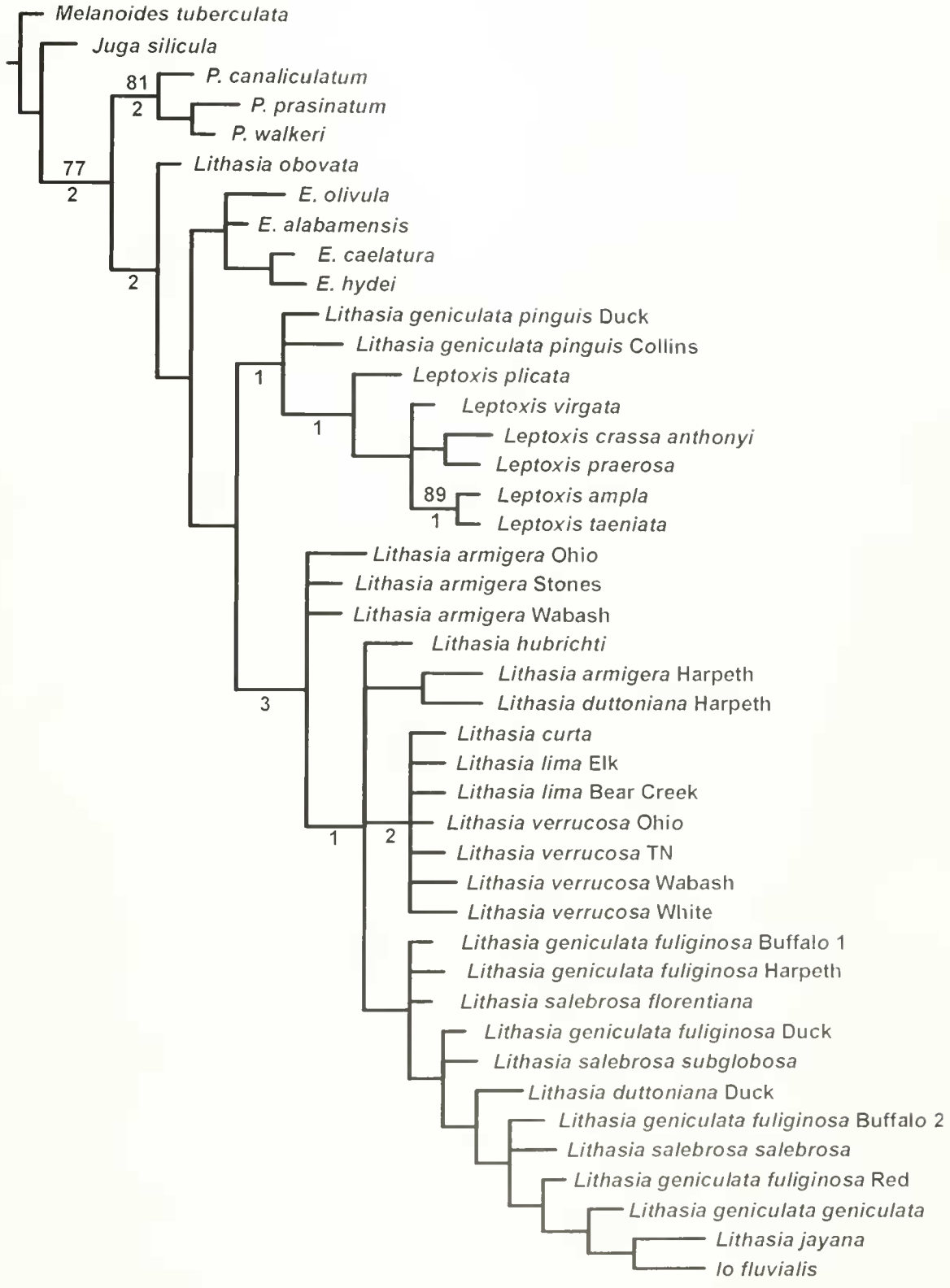


Figure 10. Cladistic analysis of *Lithasia*. Strict consensus of the 20 most parsimonious trees (107 steps, CI = 0.374) generated using shell and radula characters combined. Jackknife values ≥ 63% above nodes, number of unambiguous synapomorphies below nodes.

fusiform aperture (character 2: state 2), posterior callus on aperture (6:1), and slight anterior canalization of the aperture (8:1). Despite being well resolved, little support for any clade existed as evidenced by low jackknife values. Three other pleurocerid genera, *Elimia*, *Leptoxis*, and *Pleurocera*, were all recovered as monophyletic.

DISCUSSION

The current taxonomy of pleurocerids is based on shell characteristics, and most work on the family has focused on these characters. An extensive literature exists for the family, with most works being either wholly descriptive or taxonomic shuffling taxa among groups. This study stands as the first cladistic treatment of all currently recognized *Lithasia* species and their relationships to other pleurocerids based on shell and radula characters.

Neither analysis completely recovered the five classifications being compared. In both phylogenetic treatments *Lithasia* taxa did not form a single group, which refutes the taxonomies of Burch and Tottenham (1980), Goodrich (1940), and Turgeon et al. (1998). Tryon's (1873) groupings of the currently recognized species of *Lithasia* was also not supported, as sculptured and smooth taxa did not group separately. Davis's contention that *Lithasia* species should be considered as members of *Io* was partially supported in the parsimony analysis of all characters, where *Io* was nested deep in a clade containing most *Lithasia* taxa.

The consensus trees suggest that shell characters alone do not recover currently or historically recognized groups. However, shell and radula characters combined can be used to recover pleurocerid genera, but do not resolve species level identity well. In the total character analyses, *Elimia*, *Leptoxis*, and *Pleurocera* taxa all grouped in their respective genus. Only two *Lithasia* taxa grouped away from the others, suggesting that these two species may be misplaced. *Lithasia geniculata pinguis* was placed in *Leptoxis* (= *Aneulosa*) by Tryon (1861), and subsequently placed in *Lithasia*, where it has represented the headwaters form of the *geniculata–geniculata-fuliginosa-pinguis* complex. Based on the morphological characters examined here, *L. geniculata pinguis* should be classified as a species of *Leptoxis*. *Lithasia obovata* is the only species in the genus that occurs in the Green River drainage of Kentucky, and has included [illegible] nominal forms that are questionably *Lithasia*. [illegible] shells lack the calluses on the aperture, fusiform [illegible] have radulae most similar to *Elimia* species. [illegible] phylogenetic analysis suggests allocation of *L. obovata* [illegible] separate genus. I believe the addition of more [illegible] *Pleurocera* species or more morphological [illegible] analysis would resolve its generic designation. [illegible] remaining *Lithasia* species would be considered *Io* [illegible] oldest name for that clade. As such *Io* would be [illegible] by having a fusiform aperture (2:2), posterior [illegible] columella (6:1), and formation of canal of the [illegible] (8:2). This change would reflect the opinions of Davis (1979) regarding the two genera. Within *Lithasia*, however, individual species were not recovered, and continued analysis is required to elucidate diagnostic characters at the species level. None of the five current and historical classifications of *Lithasia* evaluated in this study are completely consistent with the analysis. Only the diagnosis of Burch (1982) is partially supported. A posterior callus on the columella (6:1) and the formation of anterior canal of the aperture (8:1–2) unite all *Lithasia* (minus *geniculata pinguis* and *obovata* plus *Io*) in the combined character analysis.

This study offers evidence refuting previous notions that shell and radula characters have limited utility in recognizing pleurocerid groups and supports the use of these characters in defining pleurocerid genera. In the most inclusive treatment of pleurocerids to date, Tryon (1873) offered an extensive discussion on the use and validity of shell characters in separating the various genera and species in the group. Tryon recognized that shell characters can vary greatly and looked towards the use of other anatomical characters to separate "natural genera" and discover corroborative shell characters for these groupings. Goodrich (1940: 1) noted that shell characters "once. . .considered immutable have proved to be secondary and more or less evanescent". Tryon (1873: liii–lv) figured some of Troschel's illustrations of radulae and commented on Stimpson's observations that shell and radula characters seem to unite pleurocerids but do little to separate constituent genera and species. It is true that gastropod radulae (Padilla, 1998) and freshwater mollusk shell characters can be plastic, often exhibiting clinal variations (e.g., Adams, 1900, 1915; Ortmann, 1920), and therefore potentially contributing homoplasy to phylogenetic analyses. Adding soft anatomy characters to a study such as this might theoretically improve the resolution of the analyses, but many characters frequently used to delineate taxa vary little among pleurocerids (Dazo, 1965) and in phylogenetic reconstructions shell characters often are less homoplastic than anatomical characters (Schander and Sundberg, 2001).

The results given here are consistent with studies employing molecular methods (Lydeard et al., 1997; Lydeard et al., 1998; Holznagel and Lydeard, 2000) to identify pleurocerid genera. In these works, *Elimia* and *Pleurocera* represent natural groups, and the morphological characters support both genera. However, Lydeard et al. (1997) and Holznagel and Lydeard (2000) showed that *Lithasia* and *Leptoxis* are non-monophyletic, though the combined morphological analysis given here supports the recognition of *Leptoxis* as a natural group. A thorough molecular study of *Lithasia*, including all of its nominal species and forms, will provide valuable information on the species composition of *Lithasia*, and subsequent character analysis will help define the diagnostic features of the genus.

ACKNOWLEDGMENTS

I would like to thank S. Ahlstedt, J. Garner, and D. Neely for specimens. M. Glaubrecht, P. Harris, C. Lydeard, and E. Strong provided helpful comments on the manuscript.

W. Holznagel and J. Nimley assisted with radula preparation and illustration, and V. Albert provided access and instruction to NONA, Winclada, and XAC. A Research Grant from Conchologists of America funded this project.

LITERATURE CITED

Adams, C. C. 1900. Variation in *Io*. Proceedings of the American Association for the Advancement of Science 49: 208–225, pls. i–xxvii.

Adams, C. C. 1915. The variations and ecological distribution of the snails of the genus *Io*. Memoirs of the National Academy of Sciences 12(2): 1–92, pls. 1–60.

Anthony, J. G. 1855. Descriptions of new species of *Anculus* and *Aneulosa*, from the western states of North America. Annual Report of the Lyceum of Natural History of New York 6: 158–160, pl. 5, figs. 20–23.

Bogan, A. E. and P. W. Parmalee. 1983. Tennessee's Rare Wildlife Volume 2: The Molluscs. 123 pp.

Bogan, A. E., J. M. Pierson and P. Hartfield. 1995. Decline in the freshwater gastropod fauna in the Mobile Basin: pp. 249–252. In: LaRoe, E. T., G. S. Farris, C. E. Puckett, P. D. Doran, & M. J. Mac (eds.), Our Living Resources: A report to the Nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington. 530 pp.

Bryant, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case of the phylogenetic taxonomy of the Carnivora. Systematic Biology 45: 174–189.

Burch, J. B. and J. L. Tottenham. 1980. North American Freshwater Snails. Species list, ranges and illustrations. Walkerana 1: 81–215.

Burch, J. B. 1982. North American Freshwater Snails. Identification keys, generic synonymy, supplemental notes, glossary, references, index. Walkerana 1: 217–365.

Clench, W. J. 1965. A new species of *Lithasia* from Mississippi. The Nautilus 79: 30–33.

Conrad, T. A. 1834a. Description of some new species of fresh water shells from Alabama, Tennessee. American Journal of Science and Arts 25(2): 338–343.

Conrad, T. A. 1834b. New freshwater shells of the United States, with coloured illustrations, and a monograph of the genus *Anculotus* of Say; also a synopsis of the American naiades. Judah Dobson, Philadelphia. 76 pp.

Davis, G. M. 1974. Report on the rare and endangered status of a selected number of freshwater Gastropoda from southeastern U.S.A. Unpublished report submitted to the Fish and Wildlife Service, U.S. Department of the Interior, Washington. 51 pp. plus maps.

Davis, G. M. and S. L. H. Fuller. 1981. Genetic relationships among recent Unionacea (Bivalvia) of North America. Malacologia 20: 217–253 + 2 appendices.

Dazo, B. C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). Malacologia 3: 1–80.

de Queiroz, K. and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Systematic Zoology 39: 307–322.

de Queiroz, K. and J. Gauthier. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449–480.

de Queiroz, K. and J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9: 27–31.

Farris, J. S., V. A. Albert, M. Kallersjö, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99–124.

Goloboff, P. A. 1998. NONA 2.0. Software published by the author, Tucuman, Argentina.

Goodrich, C. 1921. Something about *Angitrema*. The Nautilus 35: 58–59.

Goodrich, C. 1928. *Strephobasis*: a section of *Pleurocera*. Occasional Papers of the Museum of Zoology, University of Michigan, 192: 1–15, pls. 1–2.

Goodrich, C. 1940. The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan, 417: 1–21.

Gould, A. A. 1847. [Descriptions of *Melania* from the collection of the Exploring Expedition.] Proceedings of the Boston Society of Natural History 2: 222–225.

Graf, D. L. 2000. The Etheriodea revisited: a phylogenetic analysis of hyriid relationships (Mollusca: Bivalvia: Paleoheterodonta: Unionoida). Occasional Papers of the Museum of Zoology, University of Michigan 729: 1–21.

Haldeman, S. S. 1840. A monograph of the Limnaides and other freshwater univalve shells of North America. Supplement to No. 1. Dobson, Philadelphia. 3 pp.

Haldeman, S. S. 1841. A monograph of the Limnaides and other freshwater univalve shells of North America. No. 3 [Limnea]. J. Dobson, Philadelphia. 16 pp.

Heard, W. H. and R. H. Guckert. 1970. A re-evaluation of the Recent Unionacea (Pelecypoda) of North America. Malacologia 10: 333–355.

Holznagel, W. E. 1998. A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. American Malacological Bulletin 14: 181–183.

Holznagel, W. E. and C. Lydeard. 2000. A molecular phylogeny of North American Pleuroceridae (Gastropoda: Cerithioidea) based on mitochondrial 16S rDNA sequences. Journal of Molluscan Studies 66: 233–237.

Lea, I. 1831. Description of a new genus of the family Melaniana of Lamarck. Transactions of the American Philosophical Society 4: 122–124.

Lea, I. 1841a. New fresh water and land shells. Proceedings of the American Philosophical Society 2: 16–11–15.

Lea, I. 1841b. Continuation of Mr. Lea's paper on fresh water and land shells. Proceedings of the American Philosophical Society 2: 19–81–83.

Lea, I. 1842. Description of new freshwater and land shells. Transactions of the American Philosophical Society 8: 163–250 + 23 plates.

Lea, I. 1845. Description of new freshwater and land shells. Proceedings of the American Philosophical Society 4: 162–168.

Lea, I. 1852. Description of a new genus, *Basistoma*, of the family Melaniana, together with some new species of American Melaniae. Transactions of the American Philosophical Society 10: 293–302.

Lea, I. 1861a. Description of new species species of *Schizostoma*, *Aneulosa* and *Lithasia*. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 54–55.

Lea, I. 1861b. Description of forty-nine new species of the genus *Melania*. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 117–123.

Lea, I. 1868. New Unionidae, Melanidae, etc., of the United

States. Journal of the Academy of Natural Sciences 6: 340–341.

Lydeard, C. and R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeastern United States. Conservation Biology 9: 800–805.

Lydeard, C., W. E. Holznagel, J. Garner, P. Hartfield and M. Pierson. 1997. A molecular phylogeny of Mobile River drainage pleurocerid snails (Caenogastropoda: Cerithioidea). Molecular Phylogenetics and Evolution 7: 117–128.

Lydeard, C., J. H. Yoder, W. E. Holznagel, F. G. Thompson and P. Hartfield. 1998. Phylogenetic utility of the 5′-half of mitochondrial 16S rDNA gene sequences for inferring relationships of *Elimia* (Cerithioidea: Pleuroceridae). Malacologia 39: 183–193.

Lydeard, C., R. L. Minton and J. D. Williams. 2000. Prodigious polyphyly in imperiled freshwater pearly-mussels: a phylogenetic test of species and generic designations: In: Harper, E. M., J. D. Taylor and J. A. Crame (eds.) The Evolutionary Biology of the Bivalvia. Geological Society of London, Special Publication 177, pp. 145–158.

Mayden, R. L. and R. M. Wood. 1995. Systematics, species concepts, and the evolutionary significant unit in biodiversity and conservation biology. American Fisheries Society Symposium, 17: 58–113.

Melville, R. V. 1981. Opinion 1193. *Pleurocera* Rafinesque, 1818 (Gastropoda): the type species is *Pleurocerus acutus* Rafinesque in Blainville, 1824. Bulletin of Zoological Nomenclature 38: 259–265.

Müller, O. F. 1774. Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia. Vol. 2, xxxvi. Heineck et Faber, Havniae et Lipsiae, 214 pp.

Nixon, K. C. 1999. Winclada (BETA) ver. 0.9.9. Software published by the author, Ithaca.

Ortmann, A. E. 1920. Correlation of shape and station in freshwater mussels (Naiades). Proceedings of the American Philosophical Society 59(4): 269–312.

Padilla, D. K. 1998. Inducible phenotypic plasticity of the radula in *Lacuna* (Gastropoda: Littorinidae). The Veliger 2: 201–204.

Pilsbry, H. A. and S. N. Rhoads. 1896. Contributions to the zoology of Tennessee, No. 1. Mollusks. Proceedings of the Academy of Natural Sciences of Philadelphia 48: 487–506.

Rafinesque, C. S. 1820. Annals of nature, or annual synopsis of new genera and species of animals, plants, etc., discovered in North America. Pp. 10–11.

Redfield, J. H. 1854. Descriptions of new species of shells. Annual Report of the Lyceum of Natural History of New York 6: 130–132.

Reeve, L. A. 1860. Conchologia Iconica: or illustrations of the shells of molluscous animals. Lowell Reeve, London.

Say, T. 1821. Descriptions of the univalve shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia 2(1):149–179.

Say, T. 1825. Descriptions of some new species of fresh water and land shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia 5(3–4): 119–131.

Say, T. 1829. Descriptions of new terrestrial and fluviatile shells of North America (continued). New Harmony Disseminator 2(19): 291–293.

Schander, C. and P. Sundberg. 2001. Useful characters in gastropod phylogeny: soft information or hard facts. Systematic Biology 50: 136–141.

Sereno, P. C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. Systematic Biology 48: 329–351.

Stansbery, D. H. 1971. Rare and endangered freshwater mollusks in Eastern United States. In: Jorgenson, S. E. and R. E. Sharp (eds.) Proceedings of a symposium on rare and endangered mollusks (naiads) of the U.S. U.S. Fish and Wildlife Service, Department of the Interior, Washington, pp. 5–18f, 50 figs.

Stein, C. B. 1976. Gastropods. In: Endangered and threatened species of Alabama. Bulletin of the University of Alabama Museum of Natural History No. 2, Tuscaloosa, pp. 21–41.

Stein, C. B. 1978b. Comments on the proposed designation of a type species for *Pleurocera* Rafinesque, 1818. Bulletin of Zoological Nomenclature 34: 196–197.

Tryon, G. W. 1864. Synonymy of the species of Streponatidae, a family of fluvatile Mollusca, inhabiting North America. Proceedings of the Academy of Natural Sciences of Philadelphia 16: 24–48, 92–104.

Tryon, G. W. 1873. Land and Freshwater Shells of North America. Part IV. Streponatidae. Smithsonian Miscellaneous Collections 16(253), pp i–lv + 1–435.

Turgeon, D. D., J. F. Quinn Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione and G. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks (2nd edition). American Fisheries Society Special Publication 26, 526 pp. U. S. Fish and Wildlife Service Threatened and Endangered Species System. http://endangered.fws.gov. Queried May 5, 2001.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53: 11–22.

Appendix 1. Systematic list of taxa used in the cladistic analysis of the genus *Lithasia* (n = 1 for each taxon). Classification follows Turgeon et al. (1998); taxa are named as in Burch (1980). Complete locality information is available from the author. FMNH—Field Museum of Natural History; INHS—Illinois Natural History Survey; NCSM—North Carolina State Museum of Natural Sciences; UAG—University of Alabama Gastropod Collection, UMMZ—University of Michigan Museum of Zoology.

Taxon	Locality	Collection number
Family Pleuroceridae		
Genus *Elimia*		
E. alabamensis (Lea, 1861b)	Coosa River, Coosa Co., AL	NCSM-P-4658
E. caelatura caelatura (Reeve, 1860)	Choccolocco Creek, Calhoun Co., AL	NCSM-P-4659
E. hydei (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P-4663
E. olivula (Conrad, 1834a)	Alabama River, Monroe Co., AL	NCSM-P-4664
Genus *Io*		
Io fluvialis (Say, 1825)	Holston River, Sullivan Co., TN	NCSM-P-4667
Genus *Juga*		
J. silicula (Gould, 1847)	Oak Creek, Benton Co., OR	NCSM-P-4670
Genus *Leptoxis*		
L. ampla (Anthony, 1855)	Little Cahaba River, Bibb Co., AL	NCSM-P-4671
L. crassa anthonyi (Redfield, 1854)	Sequatchie River, Marion Co., AL	NCSM-P-4672
L. plicata (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P-4674
L. praerosa (Say, 1821)	Harpeth River, Davidson Co., TN	NCSM-P-4675
L. taeniata (Conrad, 1834b)	Choccolocco Creek, Talladega Co., AL	NCSM-P-4676
L. virgata (Lea, 1841a)	Chuch River, Hancock Co., TN	NCSM-P-4677
Genus *Lithasia*		
L. armigera (Say, 1821)	Wabash River, White Co., IL	INHS 23628
	Ohio River, Massac Co., IL	INHS 23632
	East Fork Stones River, Rutherford Co., TN	UAG 397
	Harpeth River, Cheatham Co., TN	UAG 572
L. curta (Lea, 1868)	Tennessee River, Lauderdale Co., AL	UMMZ 242200
L. duttoniana (Lea, 1841a)	Duck River, Maury Co., TN	UAG 402
	Harpeth River, Davidson Co., TN	UAG 405
L. geniculata geniculata (Haldeman, 1840)	Caney Fork, Dekalb Co., TN	UMMZ 51363
L. geniculata fuliginosa (Lea, 1842)	Buffalo River, Humphreys Co., TN (1)	UAG 406
	Red River, Robertson Co., TN	UAG 398
	Duck River, Maury Co., TN	UAG 403
	Buffalo River, Perry Co., TN (2)	UAG 395
	Harpeth River, Davidson Co., TN	UMMZ 53233
L. geniculata pinguis (Lea, 1852)	Collins River, Warren Co., TN	UAG 407
	Duck River, Coffee Co., TN	UAG 392
L. hubrichti Clench, 1965	Big Black River, Hinds Co., MS	FMNH 137751
L. jayana (Lea, 1841b)	Duck River, Humphreys Co., TN	UAG 573
L. lima (Conrad, 1834a)	Elk River, Limestone Co., AL	UAG 571
	Bear Creek, Colbert Co., AL	UAG 570
L. obovata (Say, 1829)	Green River, McLean Co., KY	FMNH 16219
L. salebrosa salebrosa (Conrad, 1834a)	Tennessee River, Lauderdale Co., AL	UAG 565
L. salebrosa florentiana (Lea, 1841a)	Tennessee River, Hardin Co., TN	UAG 425
L. salebrosa subglobosa (Lea, 1861a)	Tennessee River, Hardin Co., TN	UAG 416
L. verrucosa (Rafinesque, 1820)	Wabash River, White Co., IL	INHS 23629
	Ohio River, Massac Co., IL	INHS 23631
	Tennessee River, Hardin Co., TN	UAG 427
	Tennessee River, Lauderdale Co., AL	UAG 568
Genus *Pleurocera*		
P. canaliculatum filum (Lea, 1845)	Duck River, Maury Co., TN	NCSM-P-4686
P. prasinatum (Conrad, 1834a)	Yellowleaf Creek, Shelby Co., AL	NCSM-P-4689
P. walkeri Goodrich, 1928	Shoal Creek, Lauderdale Co., AL	NCSM-P-4692
Family Thiaridae		
Genus *Melanoides*		
M. tuberculata (Müller, 1774)	Drainage ditch, Gainesville, Alachua Co., FL	NCSM-P-4682

Appendix 2. Morphological characters and character states used in the cladistic analysis of the genus *Lithasia*

1. Shell shape. (0) globose, (1) conic, (2) ovately conic.
2. Aperture shape. (0) teardrop, (1) ovate, (2) fusiform.
3. Sculpture on posterior body whorl. (0) none, (1) carinate, (2) tubercles.
4. Sculpture medially on body whorl. (0) none, (1) sharp angle on body whorl, (2) tubercles.
5. Sculpture on entire body whorl. (0) none, (1) even lateral rows of small nodules, (2) costate.
6. Posterior callus on columella. (0) absent, (1) present.
7. Anterior callus on columella. (0) absent, (1) present.
8. Length of anterior canal of aperture. (0) none, (1) slight, (2) elongate.
9. Twisting of aperture anteriorly. (0) absent, (1) present.
10. Lengthening of aperture posteriorly along body whorl. (0) absent, (1) present.
11. Sculpture limited to body whorl. (0) yes, (1) no, (2) absent.
12. Length of aperture. (0) less than one-half shell length, (1) one-half shell length, (2) more than one-half shell length.
13. Cusp next to lateral tooth exteriorly. (0) absent, (1) present.
14. Shape of upper rachidian margin. (0) convex, (1) straight.
15. Length/width ratio of rachidian. (0) tooth as long as wide, (1) tooth longer than wide.
16. Length/width ratio of central rachidian denticle. (0) length and width equal, (1) longer than wide.
17. Shape of central rachidian denticle. (0) pointed, (1) blunt.
18. Location of cutting edge on main lateral cusp. (0) edge restricted to medial quarter, (1) edge restricted to medial half, (2) edge present on entire tooth.
19. Shape of main lateral cusp. (0) lamellar, (1) rectangular, (2) trapezoidal, (3) triangular.
20. Width of main lateral cusp. (0) less than one-third of cutting edge, (1) less than one-half but more than one-third of cutting edge, (2) greater than one-half of cutting edge.
21. Length/width ratio of main lateral cusp. (0) length and width equal, (1) length greater than width, (2) width greater than length.
22. Shape of leading edge of main lateral cusp. (0) pointed, (1) rounded, (2) straight.
23. Shape of marginal teeth. (0) pointed, (1) round.
24. Number of inner marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.
25. Number of outer marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.

Appendix 3. Cladistic analysis of the genus *Lithasia*. Data matrix of taxa and character states. River names follow appropriate taxon names where needed.

Lithasia armigera Ohio
Lithasia armigera Stones
Lithasia armigera Harpeth
Lithasia armigera Wabash
Lithasia curta
Lithasia duttoniana Duck
Lithasia duttoniana Harpeth
Lithasia geniculata fuliginosa Buffalo 1
Lithasia geniculata fuliginosa Buffalo 2
Lithasia geniculata fuliginosa Duck
Lithasia geniculata fuliginosa Harpeth
Lithasia geniculata fuliginosa Red
Lithasia geniculata geniculata
Lithasia geniculata puguis Duck
Lithasia geniculata puguis Collins
Lithasia
Lithasi
Lithasia
Lithasia
Lithasia
Lithasia
Lithasia sale
Lithasia salebro
Lithasia salebros
Lithasia verrucosa O
Lithasia verrucosa TN
Lithasia verrucosa Wabash
Lithasia verrucosa White
Io fluvialis

Appendix 3. Continued

Leptoxis ampla
Leptoxis crassa anthonyi
Leptoxis plicata
Leptoxis praerosa
Leptoxis taeniata
Leptoxis virgata
Elimia alabamensis
Elimia caelatura
Elimia hydei
Elimia olivula
Juga silicula
Pleurocera canaliculatum filum
Pleurocera prasinatum
Pleurocera walkeri
Melanoides tuberculata

Appendix 4. Genus *Lithasia*. Classification schemes used in comparison to cladistic hypotheses. Taxa marked with a (*) were not treated by the original author but are included in the groups based on their works (see text for explanation).

Turgeon et al., 1998	Burch and Tottenham, 1980	Goodrich, 1940	Tryon, 1873	Davis, 1974
Genus *Lithasia*	Genus *Lithasia*	Genus *Lithasia*	Genus *Anculosa*	Genus *Io*
L. armigera	Subgenus *Lithasia*	Group 1	*L. geniculata pinguis*	*Io fluvialis*
L. curta	*L. geniculata geniculata*	*L. armigera*	Genus *Angitrema*	*L. armigera*
L. duttoniana	*L. geniculata fuliginosa*	*L. duttoniana*	*L. armigera*	*L. curta*
L. geniculata	*L. geniculata pinguis*	*L. jayana*	*L. curta**	*L. duttoniana*
L. hubrichti	*L. obovata*	*L. lima*	*L. duttoniana*	*L. geniculata geniculata*
L. jayana	*L. salebrosa salebrosa*	Group 2	*L. geniculata geniculata*	*L. geniculata fuliginosa*
L. lima	*L. salebrosa florentiana*	*L. geniculata geniculata*	*L. hubrichti**	*L. geniculata pinguis*
L. obovata	*L. salebrosa subglobosa*	*L. geniculata fuliginosa*	*L. jayana*	*L. hubrichti*
L. salebrosa	Subgenus *Angitrema*	*L. geniculata pinguis*	*L. lima*	*L. jayana*
L. verrucosa	*L. armigera*	*L. salebrosa salebrosa*	*L. salebrosa salebrosa*	*L. lima*
	L. curta	*L. salebrosa florentiana*	*L. verrucosa*	*L. obovata*
	L. duttoniana	*L. salebrosa subglobosa*	Genus *Lithasia*	*L. salebrosa*
	L. hubrichti	Group 3	*L. geniculata fuliginosa*	*L. salebrosa florentiana*
	L. jayana	*L. curta*	*L. obovata*	*L. salebrosa subglobosa*
	L. lima	*L. hubrichti**	*L. salebrosa florentiana*	*L. verrucosa*
	L. verrucosa	*L. verrucosa*	*L. salebrosa subglobosa*	
		Group 4		
		L. obovata		